

Divergent apparent temperature sensitivity of terrestrial ecosystem respiration

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Abstract

Aims

Recent studies revealed convergent temperature sensitivity of ecosystem respiration (R_e) within aquatic ecosystems and between terrestrial and aquatic ecosystems. We do not know yet whether various terrestrial ecosystems have consistent or divergent temperature sensitivity. Here, we synthesized 163 eddy covariance flux sites across the world and examined the global variation of the apparent activation energy (E_a), which characterizes the apparent temperature sensitivity of R_e , and its interannual variability (IAV) as well as their controlling factors.

Methods

We used carbon fluxes and meteorological data across FLUXNET sites to calculate mean annual temperature, temperature range, precipitation, global radiation, potential radiation, gross primary productivity and R_e by averaging the daily values

over the years in each site. Furthermore, we analyzed the sites with >8 years data to examine the IAV of E_a and calculated the standard deviation of E_a across years at each site to characterize IAV.

Important Findings

The results showed a widely global variation of E_a , with significantly lower values in the tropical and subtropical areas than in temperate and boreal areas, and significantly higher values in grasslands and wetlands than that in deciduous broadleaf forests and evergreen forests. Globally, spatial variations of E_a were explained by changes in temperature and an index of water availability with differing contribution of each explaining variable among climate zones and biomes. IAV and the corresponding coefficient of variation of E_a decreased with increasing latitude, but increased with radiation and

corresponding mean annual temperature. The revealed patterns in the spatial and temporal variations of Ea and its controlling factors indicate divergent temperature sensitivity of R_e , which could help to improve our predictive understanding of R_e in response to climate change.

Keywords: activation energy, ecosystem respiration, index of water availability, interannual variability, gross primary productivity

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INTRODUCTION

Ecosystem respiration (R_e , including aboveground plant respiration and soil respiration) is a major component of terrestrial carbon cycle, which returns a large proportion of gross primary productivity (GPP) as carbon dioxide (CO_2) to the atmosphere (King *et al.* 2006; Piao *et al.* 2010). R_e is widely documented to strongly depend on temperature (Mahecha *et al.* 2010). The temperature sensitivity of R_e is therefore a major determinant that can influence the carbon loss of ecosystem and further affect the capacity of the biosphere in sequestering CO_2 under climate change. Nonetheless, there are huge differences in the magnitudes of carbon sequestration under climate change as predicted by several widely known global models (Cox *et al.* 2000; Friedlingstein *et al.* 2006), primarily due to the considerable uncertainties in constraining parameters of the temperature response of R_e (Friedlingstein *et al.* 2006; Kirschbaum 2006).

Most models use a common structure in which the effect of temperature on respiration is reflected by a Q_{10} function (the increase in respiration with a 10°C temperature increase) or a modified Arrhenius equation: $R_e = be^{-Ea/kT}$ (Lloyd and Taylor 1994), where b is a constant; k is the Boltzmann constant and T is the temperature in Kelvin. The key parameter Ea is the activation energy, which is the fundamental parameter determining the temperature sensitivity of respiration and largely determines R_e (Arrhenius 1915; Davidson and Janssens 2006). Based on this equation, some modified functions were used to extract temperature sensitivity parameters, such as the linearized Boltzmann–Arrhenius equation:

$$\ln R(T) = Ea \times (1/kT_{\text{ref}} - 1/kT) + \ln R(T_{\text{ref}})$$

In this expression, k is the Boltzmann constant (8.62×10^{-5} eV K^{-1}), and T_{ref} is a standard temperature (e.g. 15°C). The apparent activation energy (Ea) is the slope of the linear relationship between standardized temperature ($1/kT_{\text{ref}} - 1/kT$) and standardized respiration ($\ln(R/R(T_{\text{ref}}))$). By using this method, recent studies revealed a consistent temperature sensitivity of R_e across streams with different thermal history (Perkins *et al.* 2012) and even among lakes, rivers, estuaries, the open ocean and terrestrial ecosystems (Yvon-Durocher *et al.* 2012). Nevertheless, it is unclear whether the temperature sensitivity of R_e differs in various terrestrial ecosystems. Most terrestrial biogeochemical models use a fixed temperature sensitivity for respiration estimation and projection, largely because there is not much information on the spatial and temporal patterns of

temperature sensitivity of terrestrial R_e and their controlling factors (Friedlingstein *et al.* 2006; Lenton and Huntingford 2003; Luo 2007). Since the temperature sensitivity of plant respiration (Tjoelker *et al.* 2001), soil respiration (Xu *et al.* 2011) and microbial respiration (Suseela *et al.* 2011) all vary with environmental factors and biomes, as an integration of all the organisms, R_e should also be variable and sensitive to environmental factors.

A recent study demonstrated that the inherent kinetic properties of decomposition of R_e was globally convergent to 1.4, and the factors affecting the apparent temperature sensitivity of R_e are variable in space and time (Mahecha *et al.* 2010). So, it was assumed that the apparent temperature sensitivity of R_e is variable. However, it has yet to be studied what are the spatial and temporal variations in the apparent temperature sensitivity of R_e and what are the controlling factors for these variations. A comprehensive understanding of the factors which control the spatial and temporal variations in apparent temperature sensitivity on a global scale or in different climate areas and biomes is critical to better understand the temperature sensitivity of R_e .

The eddy covariance measurements of ecosystem CO_2 fluxes made at tower sites in the world offer a means by which the global pattern of temperature sensitivity can be studied and integrated on large spatial scales (Baldocchi 2008; Baldocchi *et al.* 2001). Previous analysis of the eddy covariance network, known as FLUXNET, showed a strong potential for revealing the spatial and temporal variability and controlling factors of ecosystem carbon fluxes (Baldocchi 2003, 2008; Law *et al.* 2002; Reichstein *et al.* 2007; Valentini *et al.* 2000). Therefore, we synthesized data from 163 eddy covariance sites (734 site-years) across the world and assessed the global pattern of the temperature dependence of R_e across climate areas and biomes. We quantified the key response variable, apparent Ea , and its interannual variability (IAV), as well as the related controlling factors. The specific questions addressed in this study were: (i) does Ea vary among terrestrial ecosystems? If it does, (ii) what are the magnitude, spatial variation and IAV of Ea of terrestrial R_e ? (iii) what are the major controlling factors or processes causing the spatial and IAV of Ea of R_e ?

MATERIALS AND METHODS

Site information and data processing

Carbon fluxes and meteorological data used in this analysis were taken from standardized files in the FLUXNET-LaThuile

database which includes 253 research sites of the FLUXNET network (Baldocchi 2008; Baldocchi et al. 2001). The data has been quality controlled and gap-filled by consistent methods (Moffat et al. 2007; Papale et al. 2006). We analyzed only those sites that provided at least 1 year of complete net ecosystem exchange (NEE) and meteorological data (gaps <5%). Some sites in subtropical–Mediterranean areas (including five sites in Europe and six in the western USA) were excluded because respiration in these sites was severely reduced by drought, particularly during warm seasons, resulting in an inverse relationship between respiration and temperature that could not be fitted using the Arrhenius equation. These sites are: ES-Lma, IT-Pia, IL-Yat, PT-mi1, PT-Mi₂, US-Blo, US-SO₃, US-SO₂, US-SO₄, US-Ton and US-Var. Hence, the results and conclusions in this study are only applicable to the ecosystems beyond subtropical–Mediterranean areas. Finally, a total of 163 sites with 734 site-years were used in this study to investigate the Q_{10} of R_e (see online supplementary material). The latitude ranges from 69.14°N at the Finland Kaamanen site (FI-Kaa) to −37.43°S at the Wallaby Creek (AU-Wac, see online supplementary material). The main plant functional types as defined by the International Geosphere-Biosphere Programme included in this study are: deciduous broadleaf forests (DBF), mixed forests (MF), evergreen forests (EF, including evergreen broadleaf forests (EBF) and evergreen needle leaf forests), grasslands (GR), wetlands (WET), open shrub (OSH), woody savanna (WSA) and croplands (CR) (see online supplementary material). The climatic zones of the sites include the boreal, continental temperate, subtropical and tropical areas (classified on fluxdata.org, see online supplementary material). Daily data of global radiation (R_g), air temperature and precipitation (PPT) were used together with eddy covariance fluxes of CO₂, i.e. NEE, R_e and GPP in this study.

Air temperature does not accurately reflect the temperature environment where R_e is occurring when temperature is <0°C, especially during periods of snow cover (Monson et al. 2006). Therefore, we excluded respiration measurements taken at daily mean air temperature <0°C (Graf et al. 2011). We used daily R_e rather than half-hourly values, because daily values, which integrate over diurnal cycles of photosynthesis and respiration, are more robust than half-hourly values in reflecting responses of ecosystem to temperature over the season. To determine the temperature dependence of R_e , we fitted the daily mean air temperature and R_e data to the linearized Boltzmann–Arrhenius equation mentioned above as used in recent studies (Perkins et al. 2012; Yvon-Durocher et al. 2012). We used $T_{ref} = 15^\circ\text{C}$ as a standardized temperature, which centers the inverse temperature data ($1/kT_{ref} - 1/kT$) nearly zero to make the intercept of the model $\ln(R(T_{ref}))$ equal to the rate of respiration at standardized temperature. This greatly reduces the correlation between the slope and the intercept. In this way, we minimized the confounding impacts of basal respiration on temperature sensitivity of respiration (Yvon-Durocher et al. 2012). The temperature chosen for

standardization does not substantially affect our result on E_a calculation and comparison.

We calculated site mean annual temperature (T), temperature range (T_{range}), annual PPT , annual R_g , potential radiation (R_{pot}), annual GPP and R_e by averaging the daily values over the years in each site.

IAV of E_a

We analyzed the sites with >8 years data to examine the IAV of E_a . In total, 23 sites (186 site-years, see online supplementary material) were included for the IAV study. For each year, we calculated annual values of T , PPT , R_g , R_{pot} , GPP, R_e and net ecosystem productivity. If missing daily data was >10% of the entire year data, the value of this year was indicated as missing. On average, for the 23 sites, data in 15% of the years was rejected due to insufficient daily data. The amounts of rejected years varied among sites, ranging from 12.5% (US-Hav) to 45% (IT-Col). We calculated the standard deviation of E_a across years at each site to characterize the absolute IAV. Since the values of E_a changed largely at different sites, we normalized the IAV of E_a by calculating coefficient of variation (CV, the ratio of standard deviation and mean value of E_a) to characterize the relative IAV (RIAV).

Statistical analysis

The differences of E_a among climate areas and biomes were statistically compared using a one-way analysis of variance. Mean annual air temperature (T), T_{range} (maximum – minimum daily temperature), annual PPT , annual R_{pot} and an IWA, as well as annual GPP and R_e were related to E_a with simple regressions. We defined the IWA as the ratio of annual actual evapotranspiration to potential evapotranspiration (AET/PET), where AET was directly measured by the eddy covariance towers and PET was estimated based on the Penman–Monteith equation with a zero canopy resistance (Reichstein et al. 2007). Multiple (stepwise) regressions were used to examine the main factors mentioned above in controlling the spatial variations of E_a and to quantify the degree to which the variations of E_a could be explained by these factors in different climate zones (boreal, temperate and tropical) and biomes (DBF, EF, and GR). WET, WSA, OSH and CR were excluded from the examination of the controlling factors of E_a , due to the insufficient number of sites ($n = 11, 3, 2$ and 17, respectively). A simple regression analysis was conducted to examine the relationship of IAV or RIAV with abiotic and biotic factors. The relationship was considered to be significant if $P < 0.05$. All statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, USA).

RESULTS

Spatial variation of E_a

The fitted site-level E_a showed large variation (Fig. 1a), ranging from the lowest value of 0.13 (corresponding to $Q_{10} = 0.51$ at 15°C) at site CN-Bed (39°53'N, 116°25'E, the vegetation

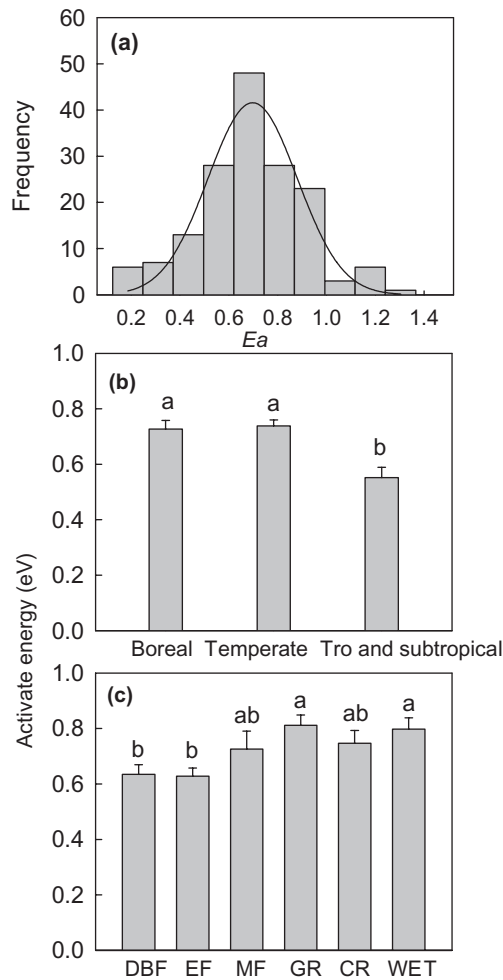


Figure 1: frequency distribution of apparent temperature sensitivity (E_a , a) and its variation among different climate areas (b) and ecosystem types (c). MF: mixed forests. The different letters indicate significant differences among the climate areas or ecosystem types.

type is EBF) to the highest value of 1.36 (corresponding to $Q_{10} = 5.47$ at 15°C) at site CN-Du1 (42°05'N, 116°67'E, the vegetation type is CR), and with a global mean value of 0.69 (corresponding to $Q_{10} = 2.8 \pm 0.9$ (SD) at 15°C). In general, E_a in cold areas was higher than that in warm areas. Tropical and subtropical climate areas had significantly lower E_a than boreal and temperate areas (Fig. 1b). GR and WET had significantly higher E_a than DBF and EF (Fig. 1c).

The standardized temperature ($1/kT_{15} - 1/kT$) and the standardized respiration ($\ln(R/R_{15})$) had consistently positive relationships with each other (Fig. 2). The slope of the relationship reflects the overall average of E_a within individual climate area or vegetation type. Tropical and subtropical areas had significantly lower slopes than boreal and temperate areas, while WET had the highest slopes and EF had the lowest slopes among the six biomes (Fig. 2).

Controlling factors of spatial variations in E_a

Globally, E_a had a positive relationship with increasing latitude, T_{range} and IWA, but negatively correlated with mean

annual air temperature (T) and potential global radiation (R_{pot}) (Fig. 3). However, the controlling factors for E_a varied with climate zones or vegetation types. In the boreal region, E_a was positively dependent on latitude and IWA, but negatively correlated with R_{pot} (Table 1). In the temperate areas, E_a also positively correlated with latitude and IWA, but negatively with T and R_{pot} (Table 1). In contrast, PPT , T_{range} and IWA appeared to be the major factors controlling E_a changes in tropical areas, which all showed a positive relationship with E_a (Table 1). For different biomes, R_{pot} was negatively correlated with E_a in the DBF, EF and GR, while latitude, T_{range} and IWA all showed positive correlations and T showed negative correlations with E_a in the EF and GR (Table 1).

IAV of E_a

IAV of E_a (measured by standard deviation) varied from 0.05 to 0.19 across the 23 sites with >8 years of data. IAV of E_a declined with increasing latitude but increased with mean annual R_g (Fig. 4a and b). The IAV of R_g , GPP and R_e all had significantly positive relationships with the IAV of E_a (Fig. 4c–f). The RIAV of E_a (measured by CV) also declined with latitude but increased with mean annual R_g , R_{pot} and air temperature (Fig. 5a–d). IAV and RIAV of radiation all had significant correlations with RIAV of E_a (Fig. 5e–f).

DISCUSSION

Global variation in E_a and its IAV

Apparent temperature sensitivity effectively reflects the overall seasonal temperature dependence of respiration at the ecosystem level, although it includes other confounding factors (e.g. seasonal dynamics) in addition to temperature (Yvon-Durocher *et al.* 2012). Actually, in recent years, the apparent temperature dependence of respiration has been widely used to estimate R_e and its temperature sensitivity (Curtis *et al.* 2005; Desai *et al.* 2005; Larsen *et al.* 2007; Piao *et al.* 2010; Reichstein *et al.* 2007; Yvon-Durocher *et al.* 2012; Zheng *et al.* 2009). Based on the metabolic theory (Brown *et al.* 2004), R_e is largely determined by the overall ecosystem biomass and the metabolic rate of that biomass (Allen *et al.* 2005). This suggests that the temperature sensitivity of R_e reflects both ecosystem's structures and its biotic and abiotic factors that interact with each other. Therefore, E_a calculated in this study represents the overall temperature sensitivity of ecosystem, including all of the ecological processes affecting CO_2 production.

Our analysis of a global CO_2 flux database suggests that there exists great spatial variation in temperature dependence of R_e (Fig. 1). The large differences in E_a among climate areas and biomes (Figs 1 and 2) indicate divergent apparent temperature sensitivity of R_e at the global scale. Our results were contrary to the previous findings on the consistent intrinsic temperature sensitivity of R_e across terrestrial ecosystems (Mahecha *et al.* 2010), stream ecosystems (Perkins *et al.* 2012) or aquatic ecosystems (Yvon-Durocher *et al.* 2012). As indicated in Mahecha *et al.* (2010), the intrinsic temperature

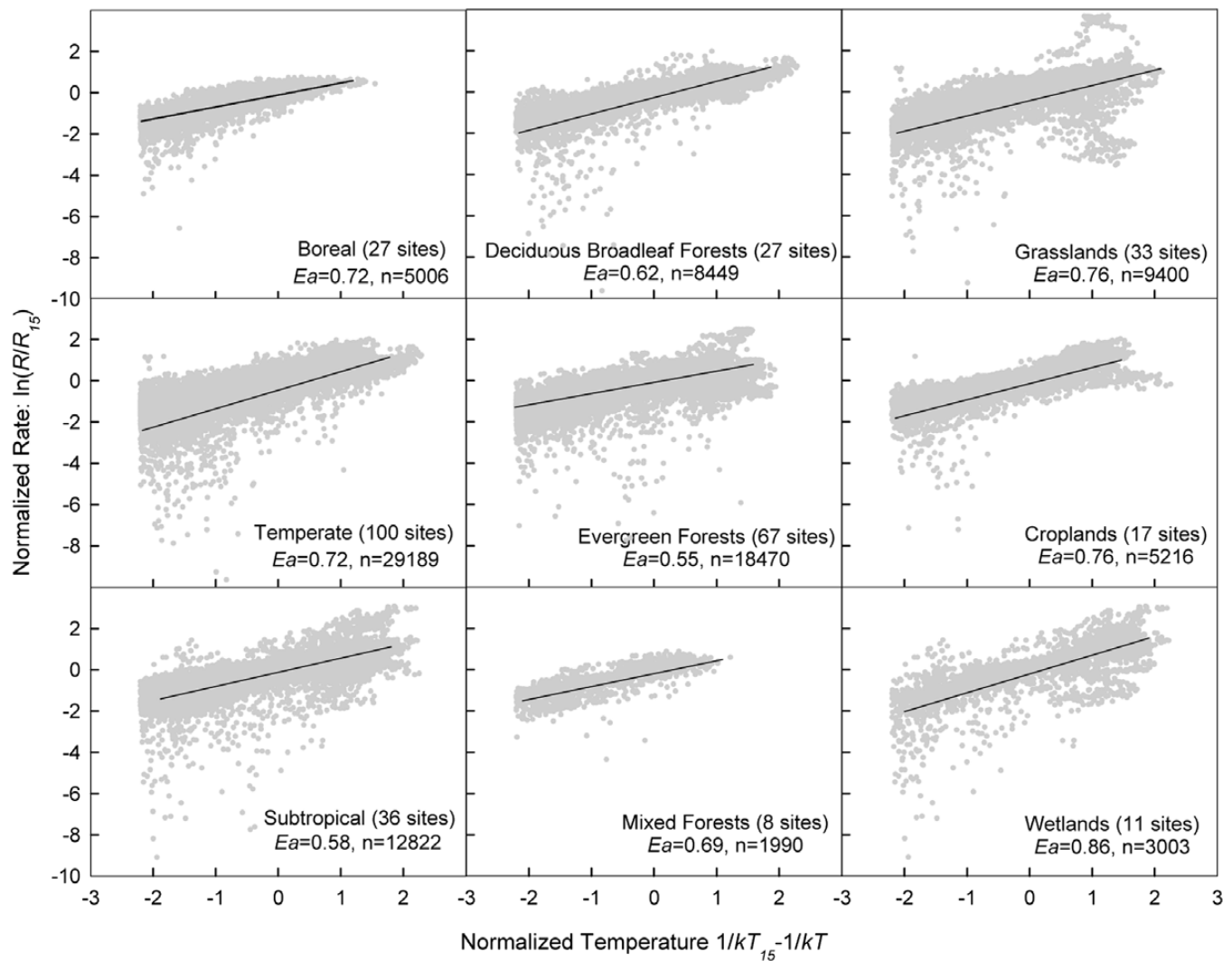


Figure 2: relationships between standardized respiration rate and standardized inverse temperature for the sites encompassing different climate areas and ecosystem types. The slope of the relationship reflects the overall average of E_a within each climate area or vegetation type.

sensitivity is consistent but the factors affecting the apparent temperature sensitivity may vary in space. Our study revealed the primary factors impacting the variations of apparent temperature sensitivity among sites. In Perkins *et al.* (2012)'s study, the stream systems had a higher heat capacity than terrestrial ecosystems, which may cause little changes in the temperature response of respiration with various thermal history (Perkins *et al.* 2012).

The higher E_a in GR and CR than in forests may be due to larger seasonal variations or dynamics in phenological phenomena and plant growth in GR and CR. Ecosystems with low mean annual temperature but large annual amplitude of temperature variation often have higher temperature sensitivity than warmer ecosystems with lower annual amplitude of temperature variation because of the difference in seasonality (Davidson *et al.* 2006). Migliavacca *et al.* (2011) reported that part of the variability in R_e was due to management in

CR and GR. For example, some management, such as fertilization and harvest, largely contributes to such abrupt changes in land cover properties, leading to large seasonal variability in R_e (Bavin *et al.* 2009). The lower E_a in tropical and subtropical areas than in temperate and boreal areas is in accordance with the variations in Q_{10} of soil respiration among the climate areas in a regional study (Zheng *et al.* 2009), which may be due to the higher temperature in tropical and subtropical areas with lower seasonal difference in temperature (and thus in plant and microbial activity).

The highly divergent E_a and its IAV revealed in this study have never been revealed before. The findings suggest that any failure of describing the spatial and temporal variability of ecosystem carbon sequestration in models may in part be due to the fact that these spatial and temporal variations of temperature sensitivity of respiration are currently not well incorporated into the global models. For example, if models

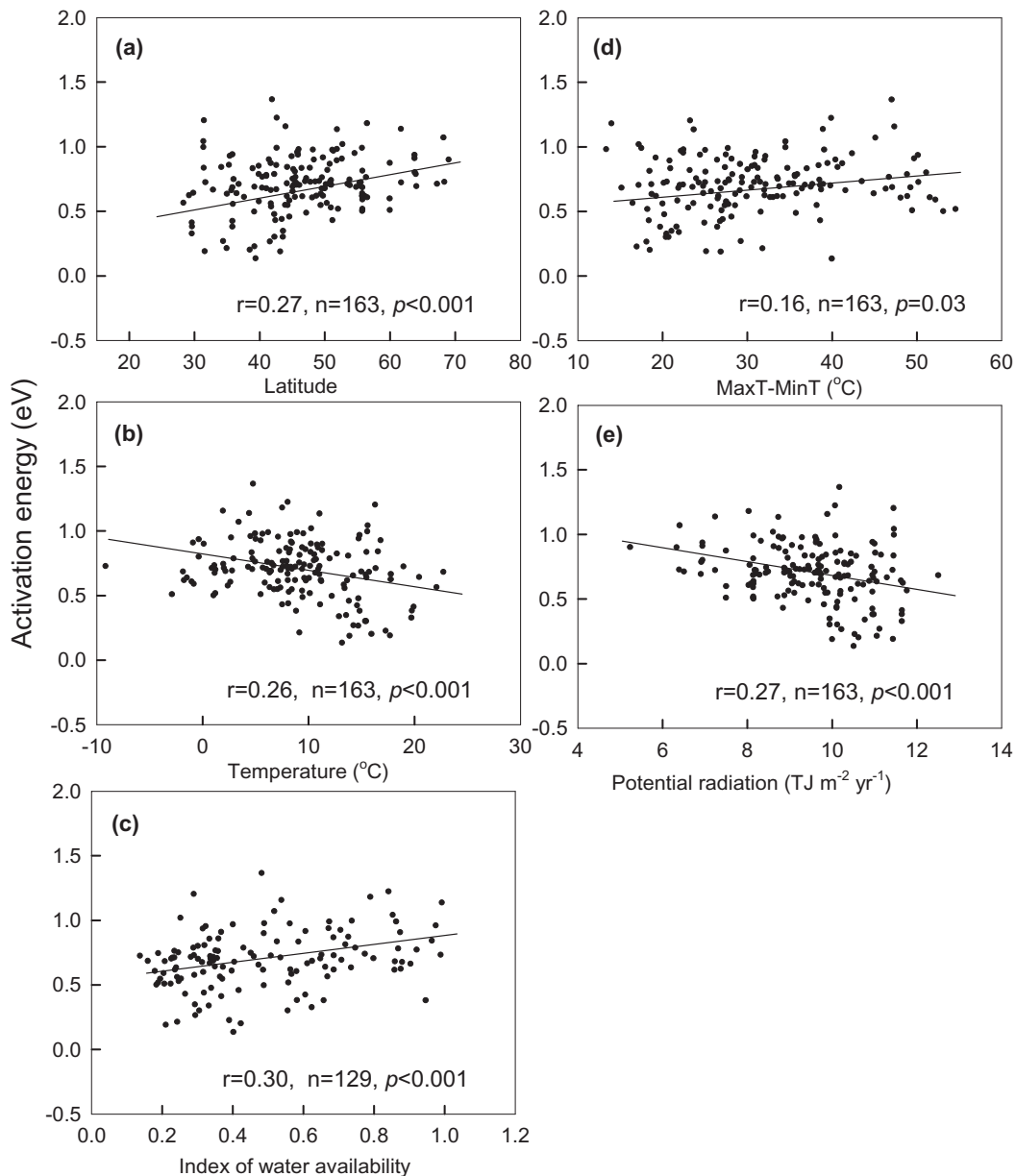


Figure 3: the relationship of apparent E_a with latitude (a), temperature range (b), mean annual temperature (c), potential radiation (d) and index of water availability (e) across the LaThuile dataset.

use a constant parameter (global mean values) for temperature sensitivity of respiration, they may overestimate R_e in tropical area but underestimate R_e in boreal area. Therefore, the global patterns of E_a and its IAV revealed in this study, based on the observed eddy flux tower data, can be helpful for improving the accuracy of model in estimating the global R_e and its response to changing climate.

Controlling factors of spatial and temporal variations in E_a

This study revealed the controlling factors of E_a , which could have potential use in biogeochemical models. Although different climate areas vary in main controlling factors of E_a , overall, water availability can largely explain the spatial variation

in E_a at the global scale (Table 1). One of the strengths of this study is to quantify the predictors for temperature sensitivity of R_e at the global scale and in different ecosystem types. Particularly interesting is the high sensitivity of E_a to water availability globally (Table 1). Previous studies paid more attention to temperature rather than to the impacts of drought on temperature sensitivity. Our findings suggest that the impacts of water on temperature sensitivity should also be considered, particularly because global warming will be accompanied by a decrease or increase in water availability (Jung *et al.* 2010). A vast majority of terrestrial ecosystems are considered to be partially water-limited, suggesting that temperature-driven decreases of temperature sensitivity may be exacerbated by limited water availability. The globally

Table 1: relationship (r) of apparent E_a with latitude (Lat , decimal degree), temperature (T , °C), PPT (mm), T_{range} (°C), GPP ($gC\ m^{-2}\ year^{-1}$), R_{pot} ($TJ\ m^{-2}\ year^{-1}$) and IWA for different climate areas and biomes

	Boreal	Temperate	Tropical	DBF	EF	GR
Lat	0.512**	0.274**	-0.246	0.231	0.425***	0.425***
T	0.305	-0.208*	-0.127	-0.029	-0.488***	-0.488***
PPT	0.079	-0.155	0.511**	-0.278	-0.065	-0.065
T_{range}	-0.220	0.035	0.662***	0.051	0.286*	0.286*
GPP	-0.229	-0.028	-0.128	0.187	-0.213	-0.213
R_{pot}	-0.512**	-0.199*	0.257	-0.391*	-0.489***	-0.489***
IWA	0.629***	0.303**	0.480**	0.224	0.291*	0.291*

*, **, ***Means the relation was significant at $p < 0.05, 0.01, 0.001$, respectively.

occurring dependence of temperature sensitivity on water availability has implications for future climate change scenarios. Changes in soil moisture affect the response of R_e to changes in air temperature in two ways: one is the direct biochemical impact on respiration, and the other is the indirect moisture effect on the temperature dependence, which will reduce the respiration-enhancing effect of higher air temperature (Reichstein et al. 2002).

Numerous studies have shown that Q_{10} of soil and plant respiration declines with increasing temperature (Chen and Tian 2005; Janssens and Pilegaard 2003; Piao et al. 2010; Tjoelker et al. 2001; Xu et al. 2011; Zheng et al. 2009), which is often described as thermal acclimation of respiration (King et al. 2006; Luo et al. 2001). It also reflects the principles of physical chemistry that Q_{10} is intrinsically temperature dependent

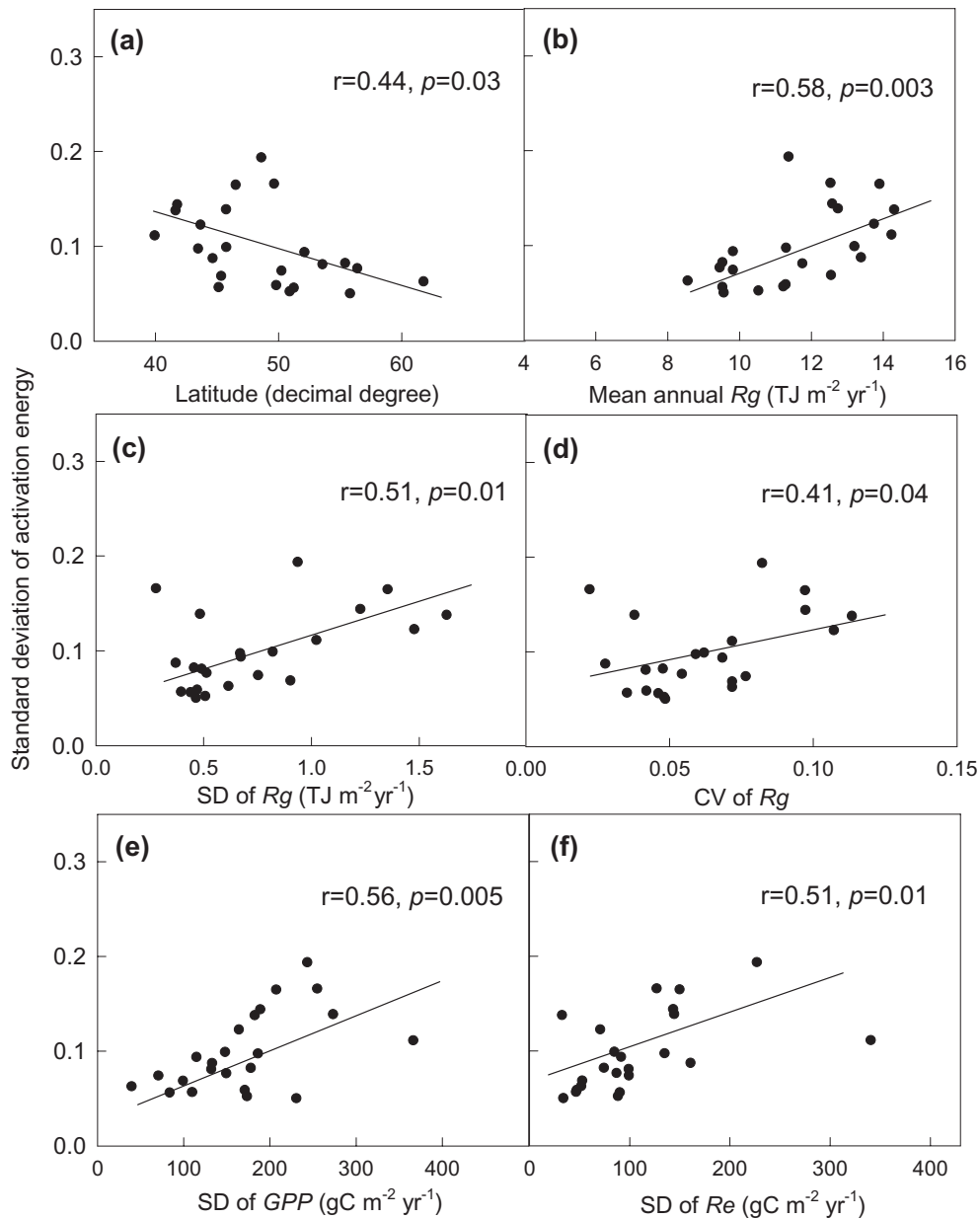


Figure 4: spatial patterns of IAV (standard deviation) of apparent E_a and their controlling factors: latitude (a), mean annual R_g (b), standard deviation of R_g (c), CV of R_g (d), standard deviation of GPP (e) and standard deviation of R_e (f).

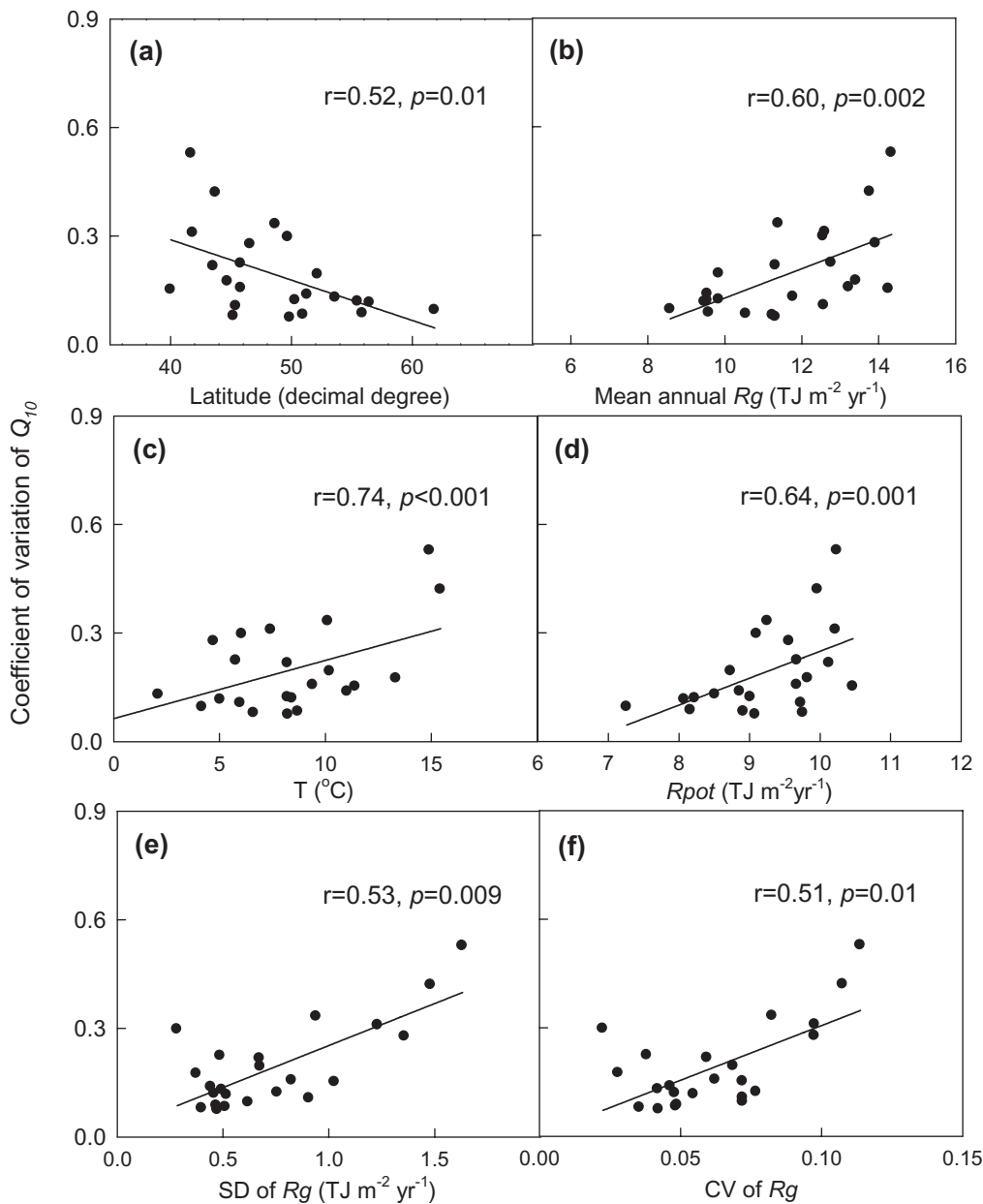


Figure 5: spatial patterns of CV of apparent E_a and their controlling factors: latitude (a), mean annual R_g (b), mean annual temperature (c), mean annual potential radiation (R_{pot}) (d), standard deviation of R_g (e) and CV of R_g (f).

when respiration follows Arrhenius kinetics (Davidson *et al.* 2006; Knorr *et al.* 2005; Perkins *et al.* 2012). Another explanation for the decreasing E_a of respiration with increasing temperature is that higher temperature may occur simultaneously with drier soil, which may decrease the temperature sensitivity of respiration, as reflected by the positive relationship between index of water availability and E_a (Fig. 5c). This is along with the declining temperature sensitivity of soil respiration with the decreasing water availability (Gaumont-Guay *et al.* 2006; Janssens and Pilegaard 2003; Peng *et al.* 2009; Reichstein *et al.* 2003), which is probably due to the decrease in substrate availability and microbial starvation under dry conditions.

The finding suggests that the limitation for decomposition rate switches from temperature to water and carbon availability under drier conditions (Davidson *et al.* 2006).

In comparing with the spatial variability, temporal variations of E_a of respiration are less addressed in previous studies (Mahecha *et al.* 2010; Perkins *et al.* 2012; Yvon-Durocher *et al.* 2012). This study revealed the large IAV of E_a and its controlling factors, which is helpful to better understand the temporal changes in the temperature sensitivity of R_c . The decreases of both IAV and the RIAV of E_a with increasing latitude (Figs 4 and 5) suggest that E_a is more sensitive to interannual environmental changes in low latitude. Considering the larger

values and lower IAV of E_a in high latitude or cold areas, northern ecosystems are most sensitive to seasonal than to interannual temperature changes. Significant correlation of IAV or RIAV between radiation and E_a indicates that interannual variations in E_a are largely due to the interannual variations in radiation. In general, radiation showed the larger RIAV at the lower latitude, which results in larger changes in IAV and RIAV of E_a . The close relationship between the variations in E_a and GPP suggests that plant carbon gain plays an important role in regulating the temporal changes of E_a . GPP directly impact R_e by providing substrate for respiration and thus is the first order factor controlling R_e (Lasslop et al. 2010). Autotrophic respiration, which is the major part of R_e , respire carbohydrates and photosynthate as substrates (Chiariello et al. 2000; Piao et al. 2010), while heterotrophic respiration is largely dependent on litter mass and soil organic carbon density, which are related to the magnitude of GPP (Raich and Tufekcioglu 2000; Yu et al. 2010).

Conclusions

We demonstrated that the apparent temperature sensitivity of terrestrial R_e changed with climate zones and vegetation types. The spatial and IAV of E_a largely varied with latitude and climate factors. This study highlights that besides temperature, soil water availability is also an important factor in influencing the temperature sensitivity of R_e . The global analysis of temperature sensitivity and its IAV improves our understanding of temperature sensitivity of R_e and helps predicting future changes in carbon cycle processes.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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